Extralimital Senegalese species during Marine Isotope Stages 5.5 and 11 in the Canary Islands (29° N): Sea surface temperature estimates

Mercedes Montesinos , Antonio J.G. Ramos , Alejandro Lomoschitz , Josep Coca , Alex Redondo , Juan F. Betancort , Joaquín Meco

Keywords:
Marine isotope stage 5.5
Marine isotope stage 11
Harpa doris
Saccostrea cucullata
Canary Islands
Sea surface temperature (SST)

ABSTRACT

The presence of *Harpa doris* Röding, 1798 in marine deposits of the last interglacial period, ~130–120 ka (marine isotope stage or MIS 5.5) in the Canary Islands (Gran Canaria, Lanzarote and Fuerteventura) enabled us to compare this occurrence with its present habitat in the Gulf of Guinea and the Cape Verde Islands, well to the south. This comparison leads to the conclusion that sea surface temperatures (SSTs) in the waters around the Canary Islands during the last interglacial period were at least 3.3 °C higher than today. *H. doris* is found in association with the large gastropod *Persististrombus latus* (Gmelin, 1791) as well as the coral *Siderastrea radians* (Pallas, 1766). The presence of these extralimital southern, warm-water species in the Canary Islands during the last interglacial period also implies a northward expansion of plankton-feeding larvae in seawater with a high chlorophyll-a content. Such conditions would require a shortening of the southern arm of the cool Canary Current that dominates the waters around the Canary Islands at present.

Marine deposits dating to ~400 ka (MIS 11) are also found on the Canary Islands. In these deposits, the presence of *Saccostrea cucullata* (Born, 1778) allows a comparison with its present habitat in the Gulf of Guinea. In this analysis, we conclude that SSTs in waters around the Canary Islands during this major interglacial period were at least 4.2 °C higher than today. Middle Pleistocene fossils of *S. cucullata* have also been found in the western Mediterranean Sea and Morocco, as well as the Cape Verde Islands. If these deposits also date to MIS 11, SST warming could have been a regional phenomenon, including much of the eastern Atlantic Ocean and Mediterranean Sea.

1. Introduction

Emergent marine deposits of the last interglacial period (marine isotope stage, or MIS 5.5, dating from ~130–120 ka) are widely distributed geographically (Muhs, 2002; Murray-Wallace, 2002; Edwards et al., 2003; Hearty et al., 2007; Dutton and Lambeck, 2012). They are usually found ~5–6 m above present sea level (apsl) on tectonically stable coasts. Using a carefully screened data set from many well-studied localities, Dutton and Lambeck (2012) computed a "global" average estimate of a paleo-sea-level of 5.5 to 9 m apsl for the last interglacial period. For this reason, and for their characteristic warm-water fauna, last interglacial deposits of MIS 5.5 are interpreted to represent greater-than-present polar ice melting, and a higher sea surface temperature (SST) than the present day. Quantification of the degree of SST increase during the last interglacial period has been estimated from deep-sea core data (Turney and Jones, 2010; Mckay et al., 2011). In mid-to-high latitudes (30° N to 70° N) of the Atlantic Ocean, warming by up to ~4 °C during MIS 5.5 has been estimated, but confirmation of this requires examination of reliable well-dated records.

Emergent marine deposits of MIS 11 (dating from ~420–360 ka, based on Helmke et al. (2008) are much less common than those of MIS 5.5, and although they are also widely distributed geographically, there is no general agreement as to the difference in sea level compared to the present day (see review in Bowen, 2010). Records from some localities indicate that MIS 11 sea level was close to present (Hearty and Kindler, 1995; Vézina et al., 1999; Murray-Wallace, 2002; Schellmann and Radtke, 2004). However, other localities provide evidence that MIS 11 sea level was ~20 m apsl (Kaufman and Brigham-Grette, 1993; Hearty et al., 1999; Hearty, 2000; Kindler and Hearty, 2000; Lundgerg and McFarlane, 2002; Olson and Hearty, 2009). This divergent point has led to different interpretations about how warm this interglacial period was (Bowen, 2010; Hearty, 2010; Muhs et al., 2012) because of the relation between sea level and ice volume. With regard to paleotemperatures, little is known of SST during MIS 11, because so few deposits have been adequately dated or have a sufficiently diverse faunal record to estimate past thermal conditions (Martrat et al., 2007; Kandiano et al., 2012). The Canary Islands (Fig. 1) are an excellent study area for addressing many of the issues regarding interglacial sea levels and SST. Deposits corresponding to both interglacial periods (MIS 5.5 and 11) have been found at elevated sites on the islands of Gran Canaria and Lanzarote (Fig. 2a and d). The island chain is distant from high-latitude high sheets of the Northern Hemisphere, where glacial isostatic adjustment (GIA) processes complicate the interpretations of sea level records (see discussion in Dutton and Lambeck, 2012). Although there is a long history of volcanic activity, the Canary Islands are distant from major plate boundaries, so tectonic activity is not as great as would be expected in many other regions. Finally, the Canary Islands are situated in a sensitive zone from the viewpoint of marine invertebrate zoogeography. At present, the islands are found in a region where there are living molluscs that range both well to the north and

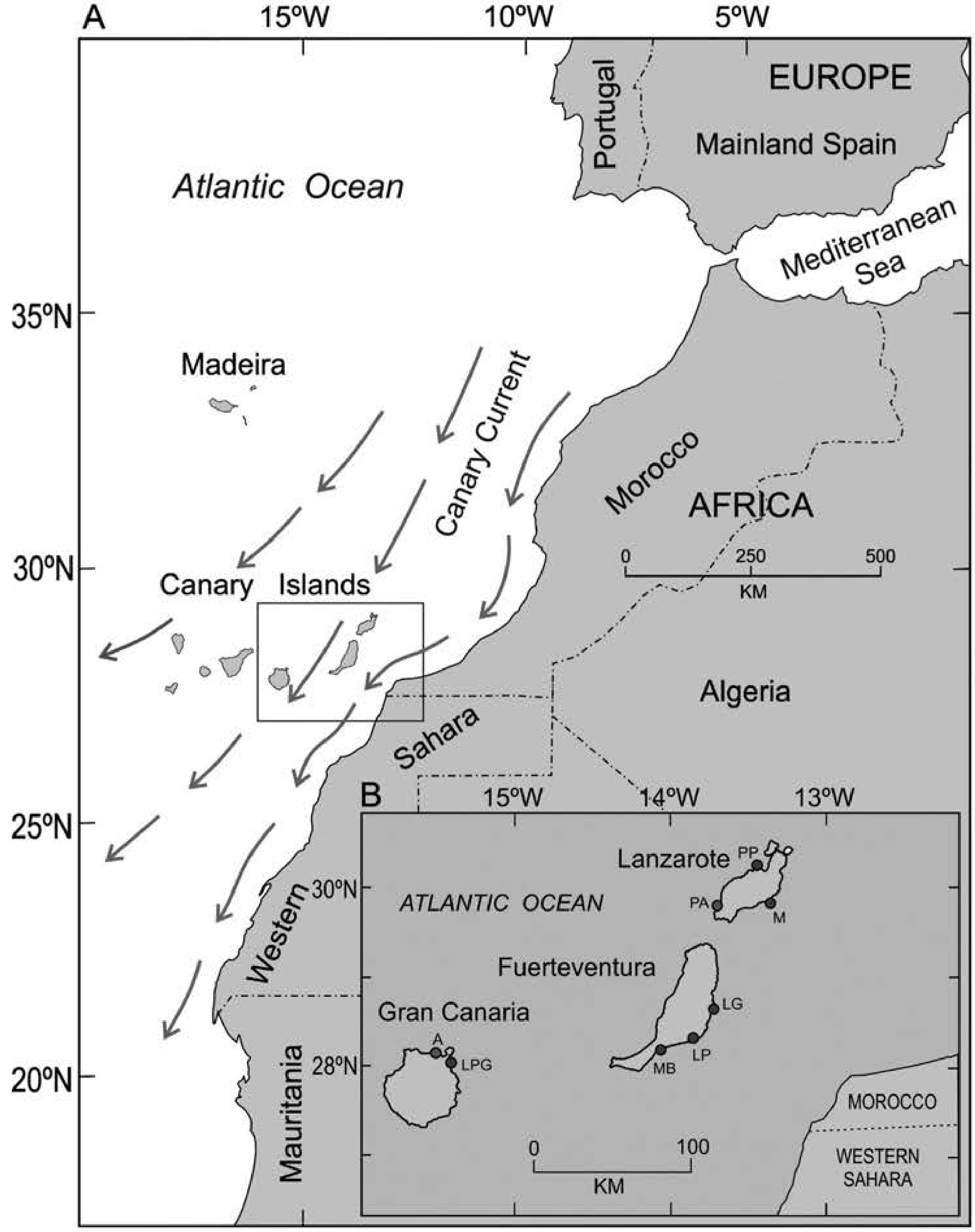

Fig. 1. (A) Location of the Canary Islands off the west coast of Africa with the Canary Current. (B) Map of western Canary Islands and locations of the marine terrace deposits from the Last Interglacial Period containing *Harpa doris* Röding fossils (red circles) and from the MIS 11 Interglacial Period with *Saccostrea cucullata* (Born) fossils (green circles). Abbreviations for localities: A, Arucas; LPG, Las Palmas de Gran Canaria; MB, Matas Blancas; LP, Las Playitas; LG, La Guirra; PA, Piedra Alta; PP, Punta Penedo; M, Matagorda.

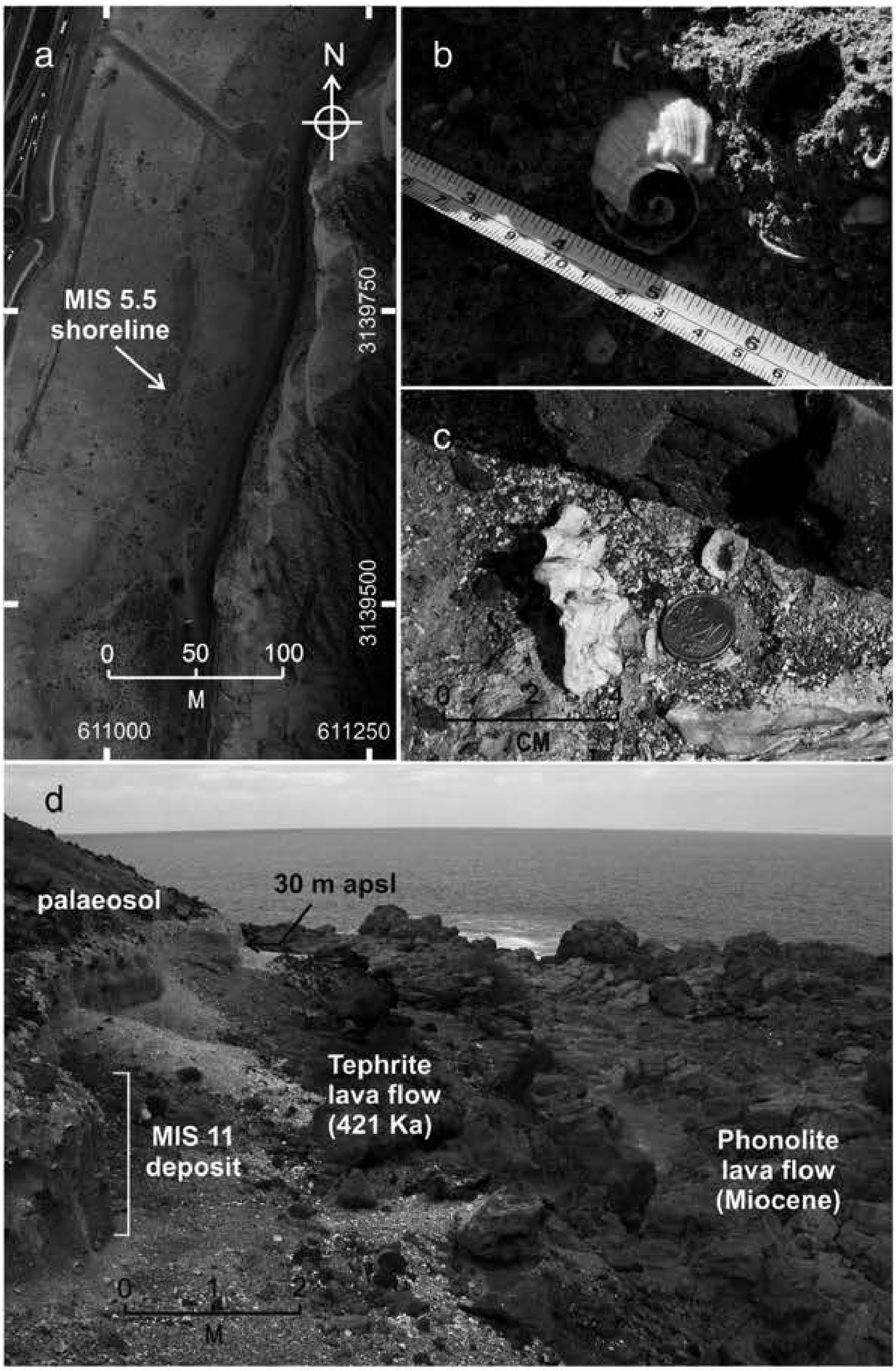

Fig. 2. (a) La Guirra locality (Fuerteventura Is.), the most tectonically stable site in the Canary Islands since the upper Pleistocene. The last Interglacial sea level MIS 5.5 is reported at 5 m apsl (red line). Source of the aerial photograph: IDE Canarias, Orto Express, Gobierno de Canarias 2013. (b) Marine deposits hosting fossil *Harpa doris* at Punta Penedo (Lanzarote) dated 130.2 ka. (c) Marine deposits hosting fossil *Saccostrea cucullata* at Cardones–Arucas Site. (d) Cardones–Arucas Site in Gran Canaria Island. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

well to the south (Meco et al., 2002). Thus, slight changes in SST will bring about a potentially dramatic change in faunal composition of the marine invertebrate community (Belanger et al., 2012; Muhs et al., 2014). In this study, parallel and complementary to the Muhs et al. (2014) study concerning U-series of corals, sea level history, and paleozoogeography of the same interglacial deposits and localities that we investigate, our goal was to quantify SST both MIS 5.5 and MIS 11 through an analysis of marine deposits in the Canary Islands and their fossils. For this purpose, we compared the geographic and paleogeographic distributions of two key species: *Harpa doris* Röding, 1798 (*H. rosea* Lamarck, 1816) from MIS 5.5 deposits and *Saccostrea cucullata* (Born, 1788) from MIS 11 (Fig. 3) deposits. *H. doris* (Fig. 2b) and *S. cucullata* (Fig. 2c) were selected as fossil species to study because both require relatively high water temperatures compared to other species in the fossil assemblages. Our approach is to use modern SST and chlorophyll-a data from the modern habitats of *H. doris* (Cape Verde Islands, Senegal, Equatorial Guinea, São Tomé, Luanda [Angola] and Ascension Island [Abbott and Dance, 2000; Rolán, 2005]) and then compare these data to the Canary Islands, where the *H. doris* fossils have been found in the MIS 5.5 deposits (Fig. 3). Many marine invertebrates

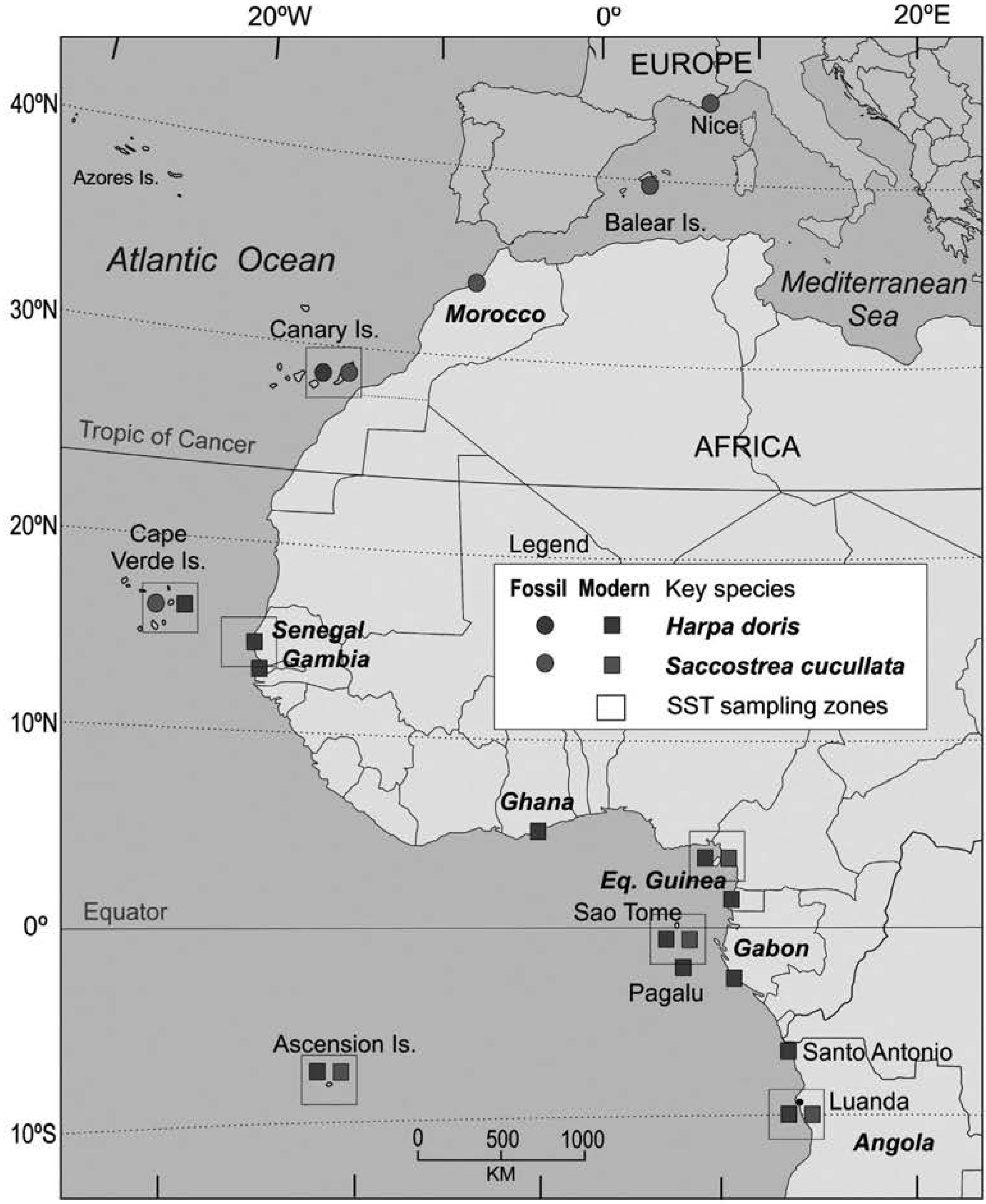

Fig. 3. Fossil and present biogeographical distribution of *Harpa doris* and *Saccostrea cucullata*. Fossil *H. doris* is only present in the Canary Islands, whereas fossil *S. cucullata* spread northward into the Mediterranean sea and southward. Both modern species are present in the inter-tropical zone, but *S. cucullata* presence is more restricted about the equator. SST (surface sea temperature) data are represented in Fig. 6.

spend the early part of their lives as meroplanktonic larvae, which depend not only on favorable water temperatures, but also on suitable food supplies. Food is available to these species in the form of phytoplankton, which contains chlorophyll-a. *H. doris* has a meroplanktonic larvae as is the case of all the members of the Genus *Harpa* (Bouchet, 2002).

For MIS 11, SST data from the modern localities where *Saccostrea cucullata* has been documented (Cameroon, Equatorial Guinea, São Tomé, Luanda (Angola) and Ascension Island) were used for purposes of comparison with *S. cucullata* fossil record of the Canary Islands (Fig. 3).

2. Methods

2.1. Paleontology

All fossils found in the study area were identified to species, including those from late Pleistocene (MIS 5.5) (Fig. 2a, b) and Middle

Pleistocene (MIS 11) deposits (Fig. 2c, d). The complete extralimital fauna for both ages of deposits on both Gran Canaria and Lanzarote are given in Muhs et al., (2014, Fig. 9, 10 and 11). All fossil samples of *Harpa doris* were successively found and collected in different localities on the Canary Islands and published previously (Meco, 1977, 1981, 1986; Meco et al., 2002, 2006, 2007). All occurrences of *H. doris* appear with *Persististrombus latus* (Gmelin, 1791), which is well-known in the Quaternary literature by its junior synonym (*Strombus bubonius* Lamarck, 1822), although the occurrence at Punta Penedo is a recent find (Meco et al., 2006). *Siderastrea radians* (Pallas, 1766) also appears in half of these MIS 5.5 sites (Meco, 1986; Meco et al., 2002, 2006). This coral has been U-series dated to ~130–120 ka on the Canary Islands (Muhs et al., 2014). Therefore the *H. doris* fossils are documented to belong to the MIS 5.5 deposits. The fossils studied by Meco (1977, 1981) have been archived in the Museo Canario de Las Palmas and the fossils studied by Meco in 1986 have been archived in the Museo de Betancuria (Fuerteventura). The rest of the samples are kept in the Paleontology Laboratory of the University of Las Palmas de Gran Canaria (ULPGC) where there is also a modern *H. doris* from the Annobon (Pagalu) Island (Meco, 1977). All the *Saccostrea cucullata* fossils studied have been documented previously (Meco et al., 2002, 2006) and come from the two MIS 11 sites, one correlated with a K/Ar dated lava flow (Meco et al., 2002) and the other containing a U-series-dated coral (Muhs et al., 2014). All these samples are part of the ULPGC Paleontological Laboratory collections. The first aim of our work has been to confirm the specific identification based on the comparison of fossil samples with modern samples and with the original descriptions and pictures, as well as to confirm their stratigraphic locations and their chronology, together their respective biogeographies.

2.2. Remote sensing

2.2.1. Study area

For this study we have selected both northern (Senegal) and southern (Luanda) boundary areas of the geographical distribution of *Harpa doris*. These northern and southern boundaries coincide with the Saharan and Namibian cold upwelling systems limits. We have also selected the area of the warmest SSTs (Equatorial Guinea-Bioko Island). Finally, we selected the Cape Verde archipelago because it is located at the Northeast latitude position of the biological *H. doris* distribution. However, the Ascension Island was selected because it is the furthest island off the African Coast and Sao Tome because it is located in the geographical Equator.

On the other hand, *Saccostrea cucullata* and *Harpa doris* coincide only in the areas of Equatorial Guinea, Sao Tome, Luanda and Ascension Island. We have also included the Canary Islands area where these species appear as fossils, so they can be compared among them.

2.2.2. SST maps

Space-based remote sensing techniques were used to determine the thermal conditions of the latitudinal bands and SST fields of the eastern Atlantic Ocean region. Temperature data are obtained from the Advanced Very High Resolution Radiometer (AVHRR) Pathfinder Version 5 SST dataset, distributed by the NASA Physical Oceanography Distributed Active Archive Center (PO.DAAC) in HDF (Hierarchical Data Format) files. The Level 3 Monthly Nighttime SST data with a spatial resolution of 4 km (0.044°) were extracted for a time period ranging from 1985 to 2009 covering a geographical area from 40° N to 30° S and 30° W to 25° E and PNG (Portable Network Graphics) images were generated using IDL® (Interactive Data Language) version 5.5.

2.2.3. Chlorophyll-a maps

Chlorophyll-a mapping provides a means for spatial analysis of food supplies for meroplanktonic larvae. Monthly chlorophyll-a concentration data were obtained from SeaWiFS level-3 SMI (Standard Mapped Image) files available from the Ocean Color Web. Data coverage is global and spatial resolution is approximately 9 km (0.087°). Files were downloaded in HDF format from NASA's Ocean Color Web servers covering the time period from 1998 to 2008. Data were extracted to a region extending from 40° N to 30° S latitude and from 30° W to 25° E longitude. PNG images (Portable Network Graphics) were generated for each month using IDL®.

2.2.4. Statistical analysis

A statistical analysis of geophysical data (SST, Chl-a) has been performed: (a) obtained basic descriptive statistic of the two geophysical variables for each of the study areas (Fig. 3): mean, maximum, minimum and the standard deviation; (b) compare the distributions of the two variables between the different areas of study. Prior to that comparison, the normality of these distributions has been studied using the Kolmogorov–Smirnov test, which results required the use of a non-parametric test. In regard to the comparison of means, the Mann–Whitney *U* test has been used, for independent samples and sensitive to the shape of distribution, to test variance homogeneity.

3. The *H. doris*, previous works

3.1. Stratigraphic location in the Canary Islands

We describe the *Harpa doris* location here only briefly because the geologic setting, fauna, and age of the same MIS 5.5 deposits and localities in the Canary Islands have been described recently (see Muhs et al., 2014). Although the number of *H. doris* individuals is low (it is very rare even in its modern localities in the Gulf of Guinea), this species has been found at the most important MIS 5.5 localities of the eastern Canary Islands including Matas Blancas (Meco, 1981) (Fig. 4b) and Las Playitas (Meco, 1986) on Fuerteventura; Punta Penedo (Meco et al., 2006) (Figs. 2b and 4d), and Matagorda (Meco, 1977) on Lanzarote (Fig. 4c) and at Las Palmas de Gran Canaria (Meco et al., 2002). Meco et al. (2002) reported eight U-series analyses and two Electron Spin Resonance (ESR) analyses performed on *Persististrombus latus* shells from the Matas Blancas deposit (see Muhs et al., 2014, Fig. 12), thought to be of last interglacial age, on Fuerteventura Island (Fig. 1). Although these analyses gave a mean age of ~128–125 ka, well within the range of MIS 5.5, it is now well established that U-series ages of molluscs (and by extension, ESR ages of molluscs as well) are not always reliable (Kaufman et al., 1971; Edwards et al., 2003). Coral is the most reliable marine fossil for U-series dating (Edwards et al., 2003). Thus, we sought corals in the marine deposits of the Canary Islands to either confirm or deny the earlier age estimates. Specimens of the coral *Siderastrea radians* were found on both Lanzarote and Gran Canaria and gave U-series ages of 130.2 $\pm$ 0.8 ka (from the north of Lanzarote) and 120.5 $\pm$ 0.8 ka (from Las Palmas de Gran Canaria). The analyses were performed on corals from the same deposits that contain *H. doris* fossils. Both ages fall within the range of coral ages that date to the peak of the last interglacial period in the Florida Keys (USA) and elsewhere (see discussion in Muhs et al., 2014) and confirm the earlier correlations of the Canary Island deposits to MIS 5.5.

3.2. Modern biogeography

The MIS 5.5 deposits of the Canary Islands have a diverse fauna, and molluscs are particularly abundant (Muhs et al., 2014). Of special significance, however, is the presence of fossils of the so-called "Senegalese" species. These include, in addition to *P. latus*, a well-known fossil on the Mediterranean coasts, the coral *S. radians*, whose present habitat is limited to the Caribbean and the Gulf of Guinea (Laborel, 1974), and the gastropod *Harpa doris* (Fig. 4a), known as *Harpa rosea* in the early specialist literature on Africa (Dunker, 1853; Nobre, 1886; Hoyle, 1887; Nobre, 1887; Smith, 1890; Lamy, 1907; Nobre, 1909; Tomlin and Shackleford, 1914; Lamy, 1923; Nicklès, 1947, 1950, 1952;

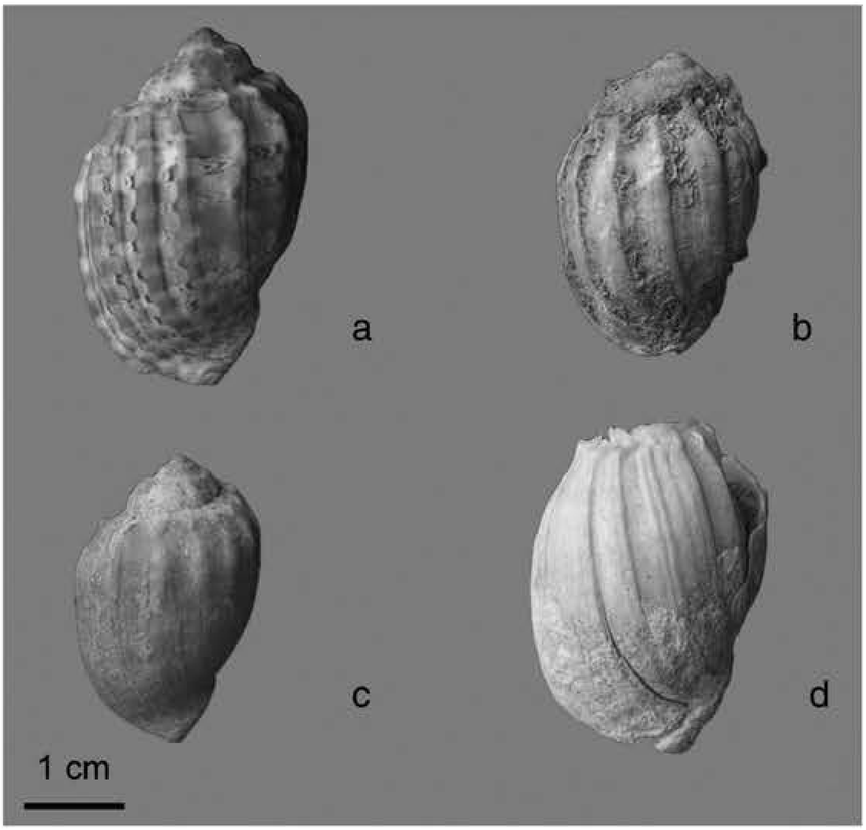

Fig. 4. (a) Present day specimen of *Harpa doris* from the island of Annobon in the Gulf of Guinea, Paleontology Laboratory Collection of Las Palmas de Gran Canaria University (No 381963). (b) Fossil specimens of *H. doris* from the marine deposits of the Last Interglacial (MIS 5.5) at Matas Blancas in Fuerteventura (No MB1977), (c) Matagorda (No M31978) and (d) Punta Penedo in Lanzarote (No P2006).

Buchanan, 1954; Knudsen, 1956; Marche-Marchad, 1956, 1958; Talavera, 1975; Meco, 1977).

Crucial to our study is a thorough understanding of the modern distribution of *Harpa doris*. Thus, we conducted a detailed search to ascertain modern occurrences of this species. Results indicate that at present, this species is found in the Cape Verde Islands (Hoyle, 1887; Knudsen, 1956; Rehder, 1973; Rolán, 2005), Ascension Island (Smith, 1890; Rehder, 1973; Abbott and Dance, 2000) Bioko or Fernando Póo (Rehder, 1973), São Tomé and Principe (Tomlin and Shackleford, 1914), Annobon (Alvarado and Álvarez, 1964; Meco, 1977), Corisco Island (Rehder, 1973), and along the African coast in Angola (Dunker, 1853; Rolán and Ryall, 1999), Gabon (Nicklès, 1952) Rio Muni or Equatorial Guinea (Rehder, 1973), Ghana (Buchanan, 1954), Gambia (Rehder, 1973), Senegal (Knudsen, 1956; Ardovini and Cossignani, 2004) and between Mauritania and Senegal (Talavera, 1975).

4. The *S. cucullata*, previous works

4.1. Stratigraphic location in the Canary Islands

The geologic setting, fauna, and age of marine deposits of Middle Pleistocene age, thought to date the MIS 11 interglacial period are found at two localities on the Canary Islands (see Muhs et al., 2014). One of these is in the Arucas–Cardones area, in northern Gran Canaria, and the other is at Piedra Alta, in western Lanzarote. The Arucas–Cardones (Fig. 2d) locality is exposed, in sea cliffs and at the mouth of a ravine, on

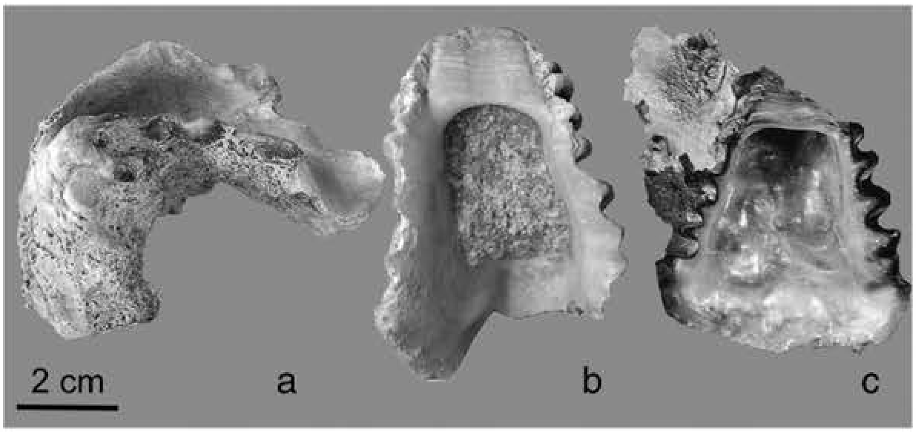

Fig. 5. (a), (b) Fossil specimen of *Saccostrea cucullata* from the marine deposits (MIS 11) of Arucas (Gran Canaria) dated by a lava flow to 421 ka (No A1131001), (c) present day specimen of *S. cucullata* from Namibe in Angola published by Gofas et al. (1985) (fig 47).

Table 1
Statistical results of SST (1985–2009) and Chlorophyll-a (1998–2007) of each selected area.

Areas SST (°C)/ Chl-a (mg/m^3)	Canary I.	Cape Verde I.	Senegal	Equatorial Guinea	Sao Tome	Luanda	Ascension I.
Number of observations	183,157/14,218	439,680/49,504	42,958/4611	99,150/7982	47,728/4651	56,565/7324	61,688/7877
Mean	20.44/0.20	23.84/0.38	23.68/7.93	27.23/3.56	26.75/0.32	24.69/2.82	25.70/0.13
Maximum	21.30/0.23	24.53/0.89	25.02/9.41	27.87/4.16	27.36/0.48	25.67/5.05	26.10/0.16
Minimum	19.69/0.17	22.84/0.26	22.69/5.92	26.75/2.83	25.98/0.26	23.58/1.55	24.69/0.10
Standard deviation	0.47/0.02	0.55/0.18	0.62/1.27	0.27/0.42	0.33/0.06	0.44/1.00	0.34/0.02

Miocene phonolite, where marine deposits overlie a lava flow from the Cardones Volcano. This lava has a pillow form, indicating that the lava cooled subaqueously. K–Ar ages of this lava are 402 ± 20 ka and 422 ± 22 ka (Meco et al., 2002). Immediately above this lava, without any paleosol, there are marine sediments, richly fossiliferous, that are found at ~30 m apsl. No corals for U-series dating were found in these deposits. However, the lack of subaerial exposure after extrusion of the pillow lava suggests that the marine deposits were laid down very shortly after the extrusion of the underlying lava. Next to this lava flow, the marine deposits occur above a paleosol containing fossil locust egg pods that indicate an arid to sub-humid climate preceding the interglacial warm–humid peak (Meco et al., 2011). Based on the K–Ar ages of the lava on which the marine sediments occur, we correlate the deposits with MIS 11.

There is somewhat more uncertainty in assessing the possible age associated with the second Middle Pleistocene site, at Piedra Alta on the island of Lanzarote. The sediments at Piedra Alta are not bedded and are poorly sorted. The deposits include large basalt clasts as well as finer-grained volcanic clasts and fossils. Meco et al. (2006) hypothesized that the sediments could represent a tsunami deposit, given the poorly sorted nature of the deposit.

The marine deposit is positioned between basalts of the Montaña Roja volcano, whose lavas have been dated by K–Ar to ~820 ka (Meco and Stearns, 1981; Meco et al., 2011) and basalts of the Montaña de Femés volcano, dated by K–Ar to ~196 ka (Meco et al., 2006) and ~160 ka (Zazo et al., 2002) and above a paleosol with innumerable fossil locust egg pods like the MIS 11 deposits on Gran Canaria. Thus, the stratigraphy and K–Ar ages require that the marine deposits must be between ~800 ka and ~200 ka and therefore *permit* a correlation with MIS 11. In addition, however, fragments of the coral *Madracis pharensis* (Heller, 1868) were recovered from the marine deposits and gave a U-series age of 481 ± 39 ka (see discussion in Muhs et al., 2014). Thus, on the basis of all available age data, we correlate the Middle Pleistocene marine deposits on Lanzarote with MIS 11 as well.

Analysis of the fauna found in the MIS 11 deposits suggests that the Arucas fauna is littoral in character, while that of Piedra Alta displays a mixture of faunal elements from various depths along with others that are completely littoral. The presence of abundant species of the genus *Patella*, unknown in the Canary Islands before MIS 11 (or in the Mediterranean before the Middle Pleistocene) indicates a paleontological age for the Piedra Alta deposits matching or very close to the deposits of Arucas, dating from MIS 11. In addition to *Saccostrea cucullata*, which we discuss in more detail below, the MIS 11 deposits in the Canary Islands also contain fossils of other species, such as *Purpurellus gambiensis* (Reeve, 1845), which at present are only found in the Gulf of Guinea.

4.2. Fossil and modern biogeography

For the comparison of MIS 11 SST to present SST, we chose the bivalve known as *Saccostrea cucullata* in the literature on Africa (Hoyle, 1887; Smith, 1890; Dautzenberg, 1912; Nicklès, 1949, 1950; Buchanan, 1954). *S. cucullata* apparently underwent a geographic migration in the Pleistocene from the western Mediterranean to the Atlantic and then southwards. In the Early Lower–Middle Pleistocene it is present in deposits near Nice, France and the Alpes-Maritimes at 72 m apsl and assigned to the Late Calabrian by Iaworsky (1963). On Mallorca, it occurs at an elevation of 70 m apsl and is considered to be Lower Pleistocene by Cuerda and Sacares (1970). It has also been reported at Larache (at 50 m apsl) and Rabat, Morocco (at 30 m apsl) referred to as being of "Messaoudian" age by Lecointre (1952). There is then a southward gap in the fossil record until the Canary Islands. In the Cape Verde Islands, it is found on Sal (at 40 m apsl) and Santiago at (7–12 m apsl), referred to as of "Anfatian" age by Lecointre (1963). It is also found in Maio (12 m apsl to 20 m apsl) and referred to as of Neotyrrhenian and Eutyrrhenian age (= last interglacial, sensu lato) by Serralheiro (1967). It is notable that in all of these deposits, *S. cucullata* and the extinct *Nucella plessisi* (Lecointre, 1952) appear together.

As with *Harpa doris* for the MIS 5.5 deposits, the modern geography of *Saccostrea cucullata* is crucial for our reconstruction of paleotemperatures for MIS 11. Hernández et al. (2011) confirm that the taxon is not found on the Canary Islands and Huber (2004) does not list it as occurring even around the Cape Verde Islands. We can confirm, however, that *S. cucullata* is found at present along the coasts of Ghana (Buchanan, 1954), Cameroon (Nicklès, 1949), Equatorial Guinea (Meco, 1977), Angola (Dautzenberg, 1912; Gofas et al., 1985; Rolán and Ryall, 1999), other parts of the coast of West Africa and adjacent islands (Hoyle, 1887), and around the islands of Bioko (Meco, 1977), Príncipe (Dohrn, 1880), São Tomé (Lamy, 1907), and Ascension (Smith, 1890) (Fig. 3). The species also lives in the Indo-Pacific province (Nicklès, 1950; Lecointre, 1952; Huber, 2004), including the Red Sea (Nicklès, 1950; Lecointre, 1952; Rusmore-Villaume, 2008). It was defined by Born (*Ostrea cucullata*, 1780, p.114, Pl.VI, Fig. 11, 12, 13) with two provenances: *Indiis* (Davila, 1767 collection—Peru) and *Insula Ascensionis* (reported by Martini, 1777). However, the Indo-Pacific history of the species has no relation to the present work, except for the

Table 2
Statistical data of warm seasons (April–September in the North Hemisphere and October–March in the South Hemisphere) of each selected area for the same periods of Table 1.

Areas SST (°C)/Chl-a (mg/m^3)	Canary I.	Cape Verde I.	Senegal	Equatorial Guinea	Sao Tome	Luanda	Ascension I.
Mean	20.77/0.17	23.78/0.26	24.64/7.97	27.43/4.76	27.22/0.32	26.22/2.70	25.41/0.11
Maximum	21.66/0.20	24.44/0.30	26.30/10.58	27.93/8.10	27.86/0.39	27.57/4.81	26.00/0.13
Minimum	19.82/0.15	22.96/0.21	23.44/4.62	26.62/3.57	26.38/0.26	24.26/1.22	24.29/0.10
Standard deviation	0.53/0.02	0.49/0.03	0.70/2.24	0.37/1.41	0.36/0.05	0.85/1.25	0.37/0.01

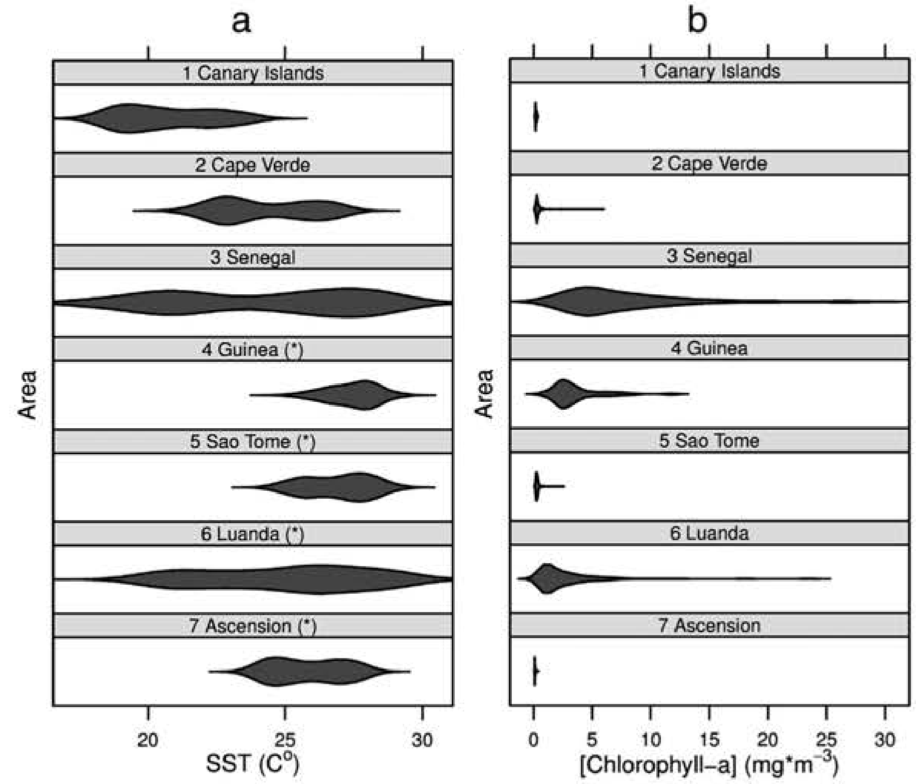

Fig. 6. (a) Sea surface temperature (SST) range for the different localities obtained from the NOAA/NASA AVHRR database (Ocean Pathfinder Sea Surface Temperature products), developed by the National Oceanographic Data Center (USA) for the time period between 1985 and 2009. An asterisk (*) (4 to 7) indicates the sites used to compare the present day SST with that of MIS 11 in the Canary Islands, while sites 2 to 7 were used for MIS 5.5. (b) Graph showing the chlorophyll-a concentration of the localities with *H. doris*. The survival and migration capacity of meroplanktonic larvae depend on the amount of chlorophyll-a available in the water. At Ascension Island, the westernmost point of the present day distribution of *Harpa doris*, the waters are oligotrophic (low chlorophyll-a content), while at the northernmost point along the African coast, Senegal, the waters are eutrophic and richer in primary production. This would confirm the origin of the *H. doris* fossils in the Canary Archipelago, closer to the phytoplankton blooms along the Northwestern African Basin.

fact that its modern zoogeography in the Indo-Pacific region indicates clearly that it is a tropical species that is found dominantly in warm waters, similar to West Africa. For the present study, however, we emphasize its Atlantic zoogeography in tropical West African waters, its Mediterranean origin from earlier in the Pleistocene (Sacco, 1897), and its fossil presence in the middle Pleistocene of Morocco and the Cape Verde Islands (Lecointre, 1952, 1963), as well as the Canary Islands (Meco et al., 2002).

5. Results

5.1. The H. doris, a new Late Pleistocene paleoclimatic indicator

A comparison of the *Harpa doris* fossil specimens from the Canary Islands with modern specimens from Annobon Island (Fig. 4a) from the ULPGC Paleontological Laboratory revealed no difference in size or shape. The holotype measures 55 mm in height and sizes for the species range between 31 mm and 77 mm (Rehder, 1973). Two of the five whole fossil specimens measure 55 mm, identical to the holotype and the others measure 47, 48 and 70 mm. The only difference between modern and fossil specimens, due to weathering was a loss of coloring in the fossils.

5.2. The S. cucullata, a new Middle Pleistocene paleoclimatic indicator

A comparison of the *Saccostrea cucullata* fossil specimens from the Canary Islands (Barranco de Cardones, Arucas, Gran Canaria) (Fig. 5a and b) with modern specimens from the Bay of Limagens (Benguela), found among rocks at a depth between 90 and 105 m (Gofas et al., 1985) (Fig. 5c), revealed no difference in size or shape except for a greater shell thickness of the Gran Canaria specimens. It is this characteristic that prompted Lecointre to give these specimens the denomination 'crassa' (*Ostrea cucullata* var. *crassa* Lecointre, 1926, p. 135 pl. 17, Fig. 1, 2, 3). Some complete specimens and several valves, from both Arucas and Piedra Alta (Lanzarote), show a characteristic heel angle, allowing their identification.

5.3. SST estimates for MIS 5.5 around the Canary Islands

Using the modern SST data and the modern distribution of the fossil taxa of interest, we can estimate the likely SST for MIS 5.5 and MIS 11 around the Canary Islands. The modern SSTs used for this study (Tables 1, 2), were recorded between 1985 and 2009 (24 years) (Fig. 6a). Application of the Kolmogorov–Smirnov test (Table 3) indicated a non-normal distribution with values ≤ 1.5. Thus, the Mann–

Table 3
Results from the Kolmogorov–Smirnov test of SST and Chl-a.

Areas	Canary I.	Cape Verde I.	Senegal	Equatorial Guinea	Sao Tome	Luanda	Ascension I.
SST Z/significance	0.841/0	0.838/0	0.835/0	0.841/0	0.808/0	0.835/0	0.841/0
Chl-a Z/significance	0.841/0	0.841/0	0.833/0	0.800/0	0.641/0	0.758/0	0.841/0

Table 4
Results from the U Mann-Whitney test of SST and Chl-a in the selected areas compared to the Canary Islands record.

Areas	Cape Verde I	Senegal	Equatorial Guinea	Sao Tome	Luanda	Ascension I.
(SST U/significance)	8018/0	21,058/0	26/0	0/0	21,111/0	282/0
(Chl-a U/significance)	2042/0	0/0	2583/0	0/0	0/0	12,587/0

Whitney *U* test was used, indicating equal statistical means for Senegal and Cape Verde (Table 4). The mean SST obtained for Canary Island waters over this 24-year period is 20.4 °C (Table 1), with a mean of 20.8 °C for the warm seasons (Table 2). Mean annual SSTs of the present habitats of *Harpa doris* (Fig. 6a) were found to be higher than those of modern waters around the Canary Islands by 3.4 °C for Cape Verde, 3.3 °C for Senegal, 6.8 °C for Equatorial Guinea, 6.3 °C for Sao Tome, 5.3 °C for Ascension Island and 4.2 °C for Luanda (Angola). These observations suggest that during the last interglacial period, SST around the Canary Islands was at least 3.3 °C higher than at the present time.

Stable isotope ($\delta^{18}O$) paleotemperatures estimated for last interglacial fossil *Persististrombus latus* from Mallorca and Tunisia (Cornu et al., 1993) are higher than modern temperatures by 7 °C or 3 °C, depending on the values assigned to sea surface salinity (unknown for the last interglacial period). However, the stable isotopic paleotemperatures for last interglacial *P. latus* fossils collected from the Matas Blancas site (Fuerteventura), indicated a SST from 4 °C to 2 °C higher than present (Bard et al., 1995).

Higher SSTs, based on the presence of fossil *Harpa doris* and other warm-water forms on the Canary Islands, require oceanographic conditions markedly different from those of today during the last interglacial period. We infer that there must have been a weakening or northward shift in the position of the Canary Current. The southward-flowing Canary Current is relatively cool and is the major control on SST around the Canary Islands at present. In order to allow the migration of *Harpa doris* and other warm-water species northwards, there would have to have been a weakening of this current, at least as far north as the Canary Islands.

The presence of *Harpa doris* in the Canary Islands during the last interglacial period not only requires warmer-than-present SSTs, but also the existence of suitable conditions for reproduction and larval dispersal during northward migration.

Following Bouchet (2002) there are two larvae types: Non-planktotrophic of *Morum* (a Genus of the Family Harpidae) protoconch consisting of 1.1–1.2 whorls and planktotrophic type of protoconch consisting of 1.8–2.8 whorls. Furthermore, Rehder (1973) described the protoconch of the Genus *Harpa* consisting of from 3 to 5 whorls and *Harpa doris* has a protoconch of 3.25 whorls. Besides, Strathmann et al. (2002) pointed out that only planktotrophic species have fairly long pelagic larval durations and feed while in the water column and consequentially they have the potential to disperse long distances. Thus, survival and migration capacity of meroplanktonic larvae depend not only on favorable temperatures, but also on the amount of phytoplankton, which can be proxied by the abundance of chlorophyll-a (Tables 1 and 2). At Ascension Island, the westernmost point of the present rday distribution of *H doris*, the waters are oligotrophic (low chlorophyll-a content), while at the northernmost point along the African coast, Senegal, the waters are eutrophic and richer in primary production (high chrolophyll-a content) (Fig. 6b). Thus, the northward expansion route of *H. doris* during the last interglacial period probably followed seawater with high chlorophyll-a content, in this case similar to that of modern waters off Senegal, and close to the phytoplankton blooms along the northwestern African coast. A primary productivity record based on coccolith accumulation rates (a proxy for phytoplankton production rate) shows high values during MIS 5.5 at 123–122 ka in the northeast Atlantic Ocean near the Azores Islands (Lototskaya et al., 1998), which supports this hypothesis. In contrast, the absolute abundance of coccoliths is low during MIS 5.5 in the equatorial Atlantic, near Ascension Island.

5.4. SST estimates for MIS 11 around the Canary Islands

Our modern analog comparison method indicates the possibility of even warmer temperatures around the Canary Islands during MIS 11. Mean annual SSTs of the present habitats of *Saccostrea cucullata*, our key species for the MIS 11 deposits, are higher than those of modern Canary Island waters by 6.8 °C for Equatorial Guinea, 6.3 °C for São Tomé, 5.3 °C for Ascension Island, and 4.2 °C for Luanda (Angola) (Table 1). It can therefore be deduced that during the MIS 11 interglacial period, the SSTs around the Canary Islands were at least 4.2 °C higher than at the present time, perhaps higher than during MIS 5.5. As with our interpretation of SSTs for MIS 5.5, warmer-than-present SSTs during MIS 11 would also require a weakening, or at least a northward shift in the position of the cool Canary Current.

6. Modern SST trends in the eastern Atlantic Ocean

An analysis of the temperature data used for this study also revealed an upward SST trend in the Gulf of Guinea over the past 24 years (Table 5). This temperature increase is most marked in Senegalese waters, perhaps indicating how these waters could have been the northward spreading path for some of the Senegalese fauna, including *Harpa doris*, during MIS 5.5. Although we recognize that this is a relatively short-term record, the upward trend agrees in general with the forecasts of the Intergovernmental Panel on Climate Change (IPCC, 2007) with regard to the consequences of climate change: warmer SSTs, but also including a rise in sea level, decreased sea-ice cover, and changes in salinity, waves and ocean circulation patterns. A consequence of these changes will likely be major faunal migrations within the marine invertebrate community. Our interpretation is that all of these phenomena occurred in the last interglacial period and prior to that, during the MIS 11 interglacial, according to data obtained from the fossil-bearing deposits of the Canary Islands. Thus, both MIS 5.5 and MIS 11 may be good analogs for what could be expected in the future.

Table 5
Mean and standard deviation of the SST (°C) values from 1985 to 2009 of selected areas.

Areas SST (°C) Mean/SD	Canary I.	Cape Verde I.	Senegal	Equatorial Guinea	Sao Tome	Luanda	Ascension I.
1985–1990	20.20/0.35	23.49/0.41	23.29/0.61	27.07/0.29	26.66/0.31	24.59/0.26	25.72/0.22
1991–1999	20.30/0.54	23.66/0.65	23.67/0.51	27.15/0.24	26.67/0.41	24.54/0.56	25.50/0.45
2000–2009	20.71/0.33	24.22/0.24	24.18/0.46	27.41/0.21	26.87/0.26	24.88/0.34	25.86/0.17

7. Conclusions

(1) *Harpa doris* Lamarck lives in the Gulf of Guinea, from Angola to Senegal, and along the islands of Annobon, São Tomé, Bioko, Ascension and Cape Verde. Fossils of this species have been found in marine deposits on the western islands of the Canary Archipelago (Gran Canaria, Fuerteventura and Lanzarote). Corals from these deposits have been dated to 120 ka and 130 ka, which correspond to the last interglacial period or MIS 5.5.

(2) A comparison of SSTs of the present day habitats of *Harpa doris* with those of modern waters around the Canary Islands reveals that SSTs around these islands during the last interglacial period were at least 3.3 °C higher than today. This last interglacial warming requires a weakening or shortening of the southern extent of the Canary Current, which at present bathes the islands with relatively cool water.

(3) Northward expansion of *Harpa doris* from Senegal would also require, in addition to warmer temperatures, a favorable food supply. We infer that the route of the plankton-feeding larvae of *H doris* from Senegal would follow seawater with high chlorophyll-a content.

(4) A single species of *Saccostrea*, *S. cucullata*, lives in the Gulf of Guinea, from Angola to Senegal, and around the islands of São Tomé, Príncipe, and Ascension. Fossils of this species have been found in marine deposits on the western islands of the Canary Archipelago (Gran Canaria and Lanzarote). These deposits have been dated to ~421 ka (Meco et al., 2002) and to ~481 ka (Muhs et al., 2014), corresponding to the MIS 11 interglacial period.

(5) A comparison of SSTs of the present day habitats of *Saccostrea cucullata* with those of Canary waters indicates that SSTs in these islands during the MIS 11 interglacial period were at least 4.2 °C higher than today. This is the first time of which we are aware that such a temperature estimate has been deduced for the MIS 11 interglacial.

(6) Some faunal elements of MIS 11 did not return to the Canary Islands during the last interglacial (MIS 5.5), suggesting a resistance to climate change and other geographical and evolutionary paths, perhaps as a result of the long duration of the MIS 11 interglacial. Nevertheless, a diverse Senegalese fauna did reach the Canary Islands and even the Mediterranean during MIS 5.5, indicating waters warmer than present.

(7) The 1985–2009 SST data for the Gulf of Guinea reveal an upward trend, especially around Senegal. This concurs broadly with the forecasts of the IPCC on the consequences of global warming. The fossil evidence presented here indicates that such warming has occurred at least twice in the relatively recent geologic past, during warm interglacial periods that may be good analogs for the future.

Acknowledgments

We would like to thank Daniel R. Muhs (U.S. Geological Survey) for critical review of the manuscript and Andrea Kourgly from the *Bibliotheken Naturhistorischen Museum Wien* for assistance, technical advice and support. The AVHRR Oceans Pathfinder SST data were obtained from the Physical Oceanography Distributed Active Archive Center (PO.DAAC) at the NASA Jet Propulsion Laboratory, Pasadena, CA. http://podaac.jpl.nasa. Researchers J. Meco and J.F. Betancort were supported by the Canary Islands CIE: Tricontinental Atlantic Campus. Chlorophyll data sets were obtained from: Feldman, G. C., C. R. McClain, Ocean Color Web, SeAWIFS Reprocessing 2010, NASA Goddard Space Flight Center. Eds. Kuring, N., Bailey, S. W. 2011. http://oceancolor.gsfc.nasa.gov/R: A language and environment for statistical computing and R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/. We wish to thank Alan Beu (GNS Sience) and the other anonymous journal reviewer, as well as the editor Thierry Corrège (Université de Bordeaux 1) who provided helpful comments on an earlier version of the paper.

References

Abbott, R.T., Dance, S.P., 2000. Compendium of Seashells. Odyssey Publishing, El Cajon, California, USA, (411 pp.).

Alvarado, R., Álvarez, J., 1964. Resultados de la expedición Peris-Álvarez a la isla de Annobón. Bol. R. Soc. Esp. Hist. Nat. 62, 265–282.

Ardovini, R., Cossignani, T., 2004. West African Seashells. L'Informatore Piceno, Ancona, (319 pp.).

Bard, E., Pätzold, J., Meco, J., Petit-Maire, N., 1995. The Canary Current: palaeotemperature from the last interglacial period. Based on $d^{18}O$ of *Strombus bubonius* from Fuerteventura Island (28°N, Canary Archipelago). Abstract 4th Climates of the Past meeting UNESCO-IUGS, EPGC. Canary Islands, June 1–5, 1995, 13–15.

Belanger, C.L., Jablonski, D., Roy, K., Berke, S.K., Krug, A.Z., Valentine, J.W., 2012. Global environmental predictors of benthic marine biogeographic structure. Proc. Natl. Acad. Sci. 109, 14046–14051.

Born, I., 1780. Testacea Musei Caesarei Vindobonensis. Joannis Pauli Kraus, Vindobonae, (XXXVI + 442 pp.).

Bouchet, P., 2002. Protoconchs, dispersal, and tectonics plates biogeography: New Pacific Species of Morum (Gastropoda: Harpidae). J. Conchol. 37, 533–549.

Bowen, D.Q., 2010. Sea level ~400 000 years ago (MIS 11): analogue for present and future sea-level? Clim. Past 6, 19–29.

Buchanan, J.B., 1954. Marine molluscs of the Gold Coast, West Africa. J. West Afr. Sci. Assoc. 1, 30–45.

Cornu, S., Pätzold, J., Bard, E., Meco, J., Cuerda-Barceló, J., 1993. Paleotemperature of the last interglacial period based on $d^{18}O$ of *Strombus bubonius* from the western Mediterranean Sea. Palaeogeogr. Palaeoclimatol. Palaeogeogr. 103, 1–20.

Cuerda, J., Sacares, J., 1970. Formaciones marinas correspondientes al límite plio-cuaternario y al Pleistoceno inferior de la costa de Lluchmayor (Mallorca). Bol. Soc. Hist. Nat. Baleares 16, 105–141.

Dautzenberg, Ph., 1912. Mission Gruvel sur la Côte Occidentale d'Afrique (1909–1910) Mollusques marins. Ann. Inst. Oceanogr. 5, 1–131.

Davila, P.F., 1767. Catalogue systématique et raisonné des curiosités de la nature et de l'art qui composent le Cabinet de M. Davila/Part 1. Briasson, Paris, (XXXV + 571 pp.).

Dohrn, H., 1880. Beiträge zur Kenntniss der Seeconchylien von West Afrika. Malacozoologische Blätter 7, 161–183.

Dunker, G., 1853. Index Molluscorum quae in itinere ad Guineam inferiorem collegit Georgius Tams Med. Dr. Theodori Fischer, Cassellis Cattorum, (74 pp.).

Dutton, A., Lambeck, K., 2012. Ice volume and sea level during the last Interglacial. Science 337, 216–219.

Edwards, R.L., Gallup, C.D., Cheng, H., 2003. Uranium-series dating of marine and lacustrine carbonates. Rev. Mineral. Geochem. 52, 363–405.

Gofas, S., Afonso, J., Pinto, J., Brandao, M., 1985. Conchas e Moluscos de Angola/ Coquillages et Mollusques d'Angola. Universidade Agostinho Neto/ Elf Aquitaine, Angola, (139 pp.).

Hearty, P.J., 2000. The Kaena highstand of Oahu, Hawaii: further evidence of Antartic ice collapse during the middle Pleistocene. Pac. Sci. 56, 65–82.

Hearty, P.J., 2010. Comment on "Sea level ~400 000 years ago (MIS 11): analogue for present and future sea—level?" by D. Q. Bowen (2010) Can the extrapolation of uplift rates from MIS 5e shorelines to MIS 11 replace direct and tangible evidence of the latter's sea-level history? Clim. Past Discuss. 6, 295–305.

Hearty, P.J., Kindler, P., 1995. Sea-level highstand chronology from stable carbonate platforms (Bermuda and the Bahamas). J. Coast. Res. 11, 675–689.

Hearty, P.J., Kindler, P., Cheng, H., Edwards, R.L., 1999. A +20 m middle Pleistocene sea-level highstand (Bermuda and the Bahamas) and partial collapse of Antartic ice. Geology 27, 375–378.

Hearty, P.J., Hollin, J.T., Neumann, A.C., O'Leary, M.J., McCulloch, M., 2007. Global sea-level fluctuations during the Last Interglaciation (MIS 5e). Quat. Sci. Rev. 26, 2090–2112.

Helmke, J.P., Bauch, H.A., Röhl, U., Kandiano, E.S., 2008. Uniform climate development between the subtropical and subpolar Northeast Atlantic across marine isotope stage 11. Clim. Past 4, 181–190.

Hernández, J.M., Rolán, E., Swinnen, F., 2011. Gastropoda: Prosobranchia. In E. Rolán (coord.). Moluscos y conchas marinas de Canarias Parte 3. ConchBooks, Hackenheim & Emilio Rolán, Vigo, pp. 54-269.

Hoyle, W.E., 1887. List of shells collected by Mr John Rattray, B. Sc., F.R.S.E. on the West Coast of Africa and the adjacent Islands. Proc. R. Phys. Soc. 9, 337–341.

Huber, M., 2004. Compendium of Bivalves. ConchBooks, Hackenheim, Germany, (901 pp.).

Iaworsky, G., 1963. Quelques coupes dans les terrains quaternaires a Monaco et dans les Alpes Maritimes. Bulletin du Musée d'Anthropologie Préhistorique de Monaco, 10, pp. 25–61.

IPCC, 2007. Summary for policymakers. Climate change 2007: working group II: impacts, adaptation and vulnerability. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., Hanson, C.E. (Eds.), IPCC Fourth Assessment Report. Cambridge University Press, Cambridge.

Kandiano, E.S., Bauch, H.A., Fahl, K., Helmke, J.P., Röhl, U., Pérez-Folgado, M., Cacho, I., 2012. The meridional temperature gradient in the eastern North Atlantic during MIS 11 and its link to the ocean–atmosphere system. Palaeogeogr. Palaeoclimatol. Palaeoecol. 333-334, 24–39.

Kaufman, D.S., Brigham-Grette, J., 1993. Aminostratigraphic correlations and paleotemperature implications, Pliocene–Pleistocene high sea level deposits, northwestern Alaska. Quat. Sci. Rev. 12, 21–33.

Kaufman, A., Broecker, W.S., Ku, T.-L., Thurber, D.L., 1971. The status of U-series methods of mollusk dating. Geochim. Cosmochim. Acta 35, 1115–1183.

Kindler, P., Hearty, P.J., 2000. Elevated marine terraces from Eleuthera (Bahamas) and Bermuda: sedimentological, petrographic, and geochronological evidence for important deglaciation events during the middle Pleistocene. Glob. Planet. Chang. 24, 41–58.

Knudsen, J., 1956. Marine Prosobranchs of Tropical West Africa (Stenoglossa). In: Bruun, A.F.R. (Ed.), Atlantide-Report Nº 4 Scientific Results of the Danish Expedition to the Coasts of Tropical West Africa 1945–1946. Danish Science Press, Copenhagen, pp. 7–110.

Laborel, J., 1974. West African reef corals an hypothesis on their origin. Proceedings of the Second InternationalCoral Reef Symposium I. , 1. Great Barrier Reef Committee, Brisbane, pp. 425–443.

Lamarck, M., 1816. Tableau Encyclopédique et Méthodique des trois régnes de la Nature. Vingt-troisième partie. Mollusques et polypes diversAgasse, Paris.

Lamy, E., 1907. Liste des coquilles marines recueillies par M. Ch. Gravier à l'île San Thome (1906). Bulletin du Museum National d'Histoire Naturelle de Paris, 13, pp. 145–154.

Lamy, E., 1923. Mollusques Testacés. Compte Rendu du Congrès des Sociétés Savantes de Paris, 1922, pp. 1–16.

Lecointre, G., 1926. Recherches géologiques dans la meseta marocaine. Institute Scientifique Chérifien, Rabat, (158 pp.).

Lecointre, G., 1952. Recherches sur le Néogene et le Quaternaire marins de la côte atlantique du Maroc. Tomo I, Stratigraphie, Tomo II, PaléontologieServices Géologique du Maroc, Paris, (198 pp. and 174 pp.).

Lecointre, G., 1963. Sur les terrains sédimentarires de l' île de Sal avec remarque sur les Îles Santiago et Maio (Archipel du Cap Vert). García de Orta Lisboa, 2, pp. 275–289.

Lototskaya, A., Ziveri, P., Ganssen, G.M., van Hinte, J.E., 1998. Calcareous nannofloral response to Termination II at 45°N, 25°W (northeast Atlantic). Mar. Micropaleontol. 34, 47–70.

Lundgerg, J., McFarlane, D., 2002. Isotope stage 11 sea level in the Netherlands Antilles. Geological Society of America. Annual Meeting Paper 9-8.

Marche-Marchad, I., 1956. Sur une collection de coquilles marines provenant de l'Archipel du Cap-Vert. Bulletin de l'I.F.A.N, 18, pp. 39–74.

Marche-Marchad, I., 1958. Nouveau Catalogue de la Collection de Mollusques testacés marin de L'IFAN. Institut Francais d'Afrique Noir, IFAN, Dakar, (64 pp.).

Martini, F.H.M., 1777. Neues Systematisches Conchylien Cabinet. , 3. G.N. Raspe, Nurberg.

Martrat, B., Grimalt, J.O., Shackleton, N.J., de Abreu, L., Hutterli, M.A., Stocker, T.F., 2007. Four climate cycles of recurring deep and surface water destabilizations on the Iberian margin. Science 317, 502–507.

McKay, N.P., Overpeck, J.T., Otto-Bliesner, B.L., 2011. The role of ocean thermal expansión in Last Interglacial sea level rise. Geophys. Res. Lett. 38, L14605. http://dx.doi.org/10.1029/2011GL048280.

Meco, J., 1977. Paleontología de Canarias I: Los Strombus neógenos y cuaternarios del Atlántico euroafricano (taxonomía, bioestratigrafía y paleoecología). Cabildo Insular de Gran Canaria, Las Palmas-Madrid, (142 pp.).

Meco, J., 1981. Neogasterópodos fósiles de las Canarias Orientales. Anu. Estud. Atlánticos 27, 606–607.

Meco, J., 1986. Climatic change in the Canary Islands during Upper Pleistocene. Travaux et Documents de l'ORSTOM, 197, pp. 301–304.

Meco, J., Stearns, C.H., 1981. Emergent littoral deposits in the Eastern Canary Islands. Quat. Res. 15, 199–208.

Meco, J., Guillou, H., Carracedo, J.C., Lomoschitz, A., Ramos, A.J.G., Rodríguez Yánez, J.J., 2002. The maximum warmings of the Pleistocene world climate recorded in the Canary Islands. Palaeogeogr. Palaeoclimatol. Palaeoecol. 185, 197–210.

Meco, J., Betancort, J.F., Scaillet, S., Guillou, H., Lomoschitz, A., Carracedo, J.C., Petit-Maire, N., Cilleros, A., Soler-Onís, E., Meco, J.M., 2006. Paleoclimatología del Neógeno en las Islas Canarias. Geliense, Pleistoceno y Holoceno. Ministerio de Medio Ambiente. Universidad de Las Palmas de Gran Canaria, Madrid-Las Palmas, (204 pp.).

Meco, J., Scaillet, S., Guillou, H., Lomoschitz, A., Carracedo, J.C., Ballester, J., Betancort, J.F., Cilleros, A., 2007. Evidence for long-term uplift on the Canary Islands from emergent Mio-Pliocene littoral deposits. Glob. Planet. Chang. 57, 222–234.

Meco, J., Muhs, D.R., Fontugne, M., Ramos, A.J.G., Lomoschitz, A., Patterson, D., 2011. Late Pliocene and Quaternary Eurasian locust infestations in the Canary Archipelago. Lethaia 44, 440–454.

Muhs, D.R., 2002. Evidence for the timing and duration of the Last Interglacial Period from high-precision uranium-series ages of corals on tectonically stable coastlines. Quat. Res. 58, 36–40.

Muhs, D.R., Pandolfi, J.M., Simmons, K.R., Schumann, R.R., 2012. Sea-level history of past interglacial periods from uranium-series dating corals, Curaçao, Leeward Antilles islands. Quat. Res. 78, 157–169.

Muhs, D.R., Meco, J., Simmons, K., 2014. Uranium-series ages of corals, sea level history, and palaeozoogeography, Canary Islands, Spain: an exploratory study for two Quaternary interglacial periods. Palaeogeogr. Palaeoclimatol. Palaeoecol. 394, 99–118.

Murray-Wallace, C.V., 2002. Pleistocene coastal stratigraphy, sea-level higstands and neotectonism of the southern Australian passive continental margin—a review. J. Quat. Sci. 17, 469–489.

Nicklès, M., 1947. La collection de Mollusques testacés de l'I.F.A.N. Institute Français d'Afrique Noire, Dakar, (23 pp.).

Nicklès, M., 1949. Mollusques marins de la région de Kribi. Etudes Camerounaises 2, 113–118.

Nicklès, M., 1950. Mollusques testacés marins de la Côte occidentale d'Afrique. Manuels ouest-africainsPaul Lechevalier, Paris, (269 pp.).

Nicklès, M., 1952. Mollusques testacés marins du littoral de l'A.E.F. J. Conchyliologie Paris 92, 143–154.

Nobre, A., 1886. Exploraçao scientifica da Ilha de S. Thomé. Conchas terrestres e marinhas recolhidas pelo Sr. Adolpho Moller na Ilha de S. Thomé en 1885. Bol. Soc. Geogr. Lisb. 4, 1–4.

Nobre, A., 1887. Remarques sur la faune malacologique marine des possessions portugaises de l'Afrique occidentale. J. Sci. Math. Phys. Nat. 46, 1–14.

Nobre, A., 1909. Matériaux pour l'étude de la faune malacologique des possessions portugaises de l'Afrique occidentale. Bull. Soc. Portugaise Sci. Nat. 2, 1–108.

Olson, S.L., Hearty, P.J., 2009. A sustained +21 m sea-level highstand during MIS 11 (400 ka): direct fossil and sedimentary evidence from Bermuda. Quat. Sci. Rev. 28, 271–285.

Rehder, H.A., 1973. The family *Harpidae* of the world. Indo-Pacific Mollusca 3, 207–272.

Rolán, E., 2005. Malacological Fauna From the Cape Verde Archipelago. Conchbooks, Vigo, (482 pp.).

Rolán, E., Ryall, P., 1999. Checklist of the Angolan molluscs/Lista de los Moluscos marinos de Angola. Reseñas Malacológicas 10, 1–132.

Rusmore-Villaume, M.L., 2008. Seashells of the Egyptian Red Sea. The American University in Cairo Press, Cairo–New York, (307 pp.).

Sacco, F., 1897. I Molluschi di Terreni Terziarii del Piamonte e della Liguria. Parte XXIII. Pelecypoda (Ostreidae, Anomiidae e Dimydae)Carlo Clausen, Torino, (68 pp.).

Schellmann, G., Radtke, U., 2004. A revised morpho- and chronostratigraphy of the late and middle Pleistocene coral reef terraces on Southern Barbados (West Indies). Earth Sci. Rev. 64, 157–187.

Serralheiro, A., 1967. Sobre as praias antigas de algumas ilhas de Cabo Verde. García de Orta, 15, pp. 123–138.

Smith, E.A., 1890. Report on the marine Mollusca of Ascension Island. Proc. Zool. Soc. London 22, 317–322.

Strathmann, R., Hugues, T.P., Kuris, A.M., Lindeman, K.C., Morgan, S.G., Pandolfi, J.M., Warmer, R.R., 2002. Evolution of local recruitment and its consequences for marine populations. Bull. Mar. Sci. 70, 377–396 (Suppl.).

Talavera, F.G., 1975. Moluscos de sedimentos de la plataforma continental de Mauritania. Bol. Inst. Esp. Oceanogr. 192, 3–18.

Tomlin, J.R., Shackleford, L.J., 1914. The marine mollusca of Sao Thomé. J. Conchol. 14, 239–256.

Turney, C.S.M., Jones, R.T., 2010. Does the Agulhas Current amplify global temperatures during super-interglacials? J. Quat. Sci. 25, 839–843.

Vézina, J., Jones, B., Ford, D., 1999. Sea-level highstands over the last 500,000 years: evidence from the Ironshore Formation on Grand Cayman, British West Indies. J. Sediment. Res. 69, 317–327.

Zazo, C., Goy, J.L., Hillaire-Marcel, C., Gillot, P., Soler, V., González, J.A., Dabrio, C.J., Ghaleb, B., 2002. Raised marine sequences of Lanzarote and Fuerteventura revisited. A reappraisal of relative sea-level changes and vertical movements in the eastern Canary Islands during the Quaternary. Quat. Sci. Rev. 21, 2019–2046.